flower stalk, at height of one meter above the ground, 1.5-6 inches, average 3.3 inches; length of panicle 3-11.5 feet, average 6.5 feet; diameter of panicle 1-3 feet, average 2 feet; length of leaves 17-46 inches, average 29 inches.

The largest individuals of Yucca Whipplei occur in this subspecies. It is distinguishable from the other solitary form of the species by the size of its inflorescence. In all dimensions measured the inflorescence of subsp. Parishii is nearly twice as large as the inflorescence of subsp. typica. The subspecies is found on the western slopes of the San Bernardino and San Gabriel mountains where it occurs from 1000 to 8000 feet elevation. At lower elevations it occurs with the chaparral and coastal sage formations, at higher elevations it ranges well into the montane forest.

Department of Botany, University of California, Los Angeles, September 26, 1940.

CERTAIN NORTH AND SOUTH AMERICAN DISTRIBUTIONS IN SCIRPUS

Alan A. Beetle

Recent studies on collections of the cyperaceous genus Scirpus L. obtained in South America by the University of California Botanical Expedition to the Andes has revealed a surprisingly high degree of relationship between the species of this genus in the two hemispheres. Although one species is endemic to the California flora a large number of the species is wide ranging making it necessary to study both near and distant floras to discover their true affinities. The genus has many American species. Nothing approaching a general statement may as yet be given for their distribution. Some range widely, whereas others are very narrowly endemic or occupy discontinuous ranges.

The California flora contains sixteen species of Scirpus as follows: S. microcarpus Presl, S. Congdoni Britton, S. criniger Gray, S. paludosus A. Nels., S. robustus Pursh, S. fluviatilis (Torr.) Gray, S. acutus Muhl., S. validus L., S. californicus (C. A. Mey.) Steud., S. Olneyi Gray, S. americanus Pers., S. nevadensis Wats., S. Clementis Jones, S. carinatus Gray, S. setaceus L. and S. cernuus Vahl. The species known from Argentina were recently well organized by Barros (1). Without following Barros too closely the following entities may be recognized: S. deserticola Phil., S. giganteus Kunth, S. paludosus, S. asper Presl, S. cubensis Poepp. & Kunth, S. californicus, S. validus, S. Olneyi, S. americanus, S. nevadensis, S. atacamensis (Phil.) Boeckl., S. rigidus Boeckl., S. macrolepis Boeckl., S. cernuus and S. inundatis Poir. Scirpus Clementis, S. criniger and S. Congdoni are endemic in the North American flora while S. atacamensis, S. rigidus, S. macrolepis, S. giganteus and S. deserticola are

1941]

endemic in South America. Nearly fifty per cent of the species comprising these two lists occur both in California and in Argentina. An analysis of the distribution of those species which occur both north and south of the equator should afford some information concerning the interchange of species in general between the

In Scirpus, the section Baeothryon consists of perennials with spikelets uniformly single, terminal, style 3-fid, and achene smooth, brown. It comprises eight species and one variety, namely S. hudsonianus (Michx.) Fern., S. planifolius Muhl., S. Clintonii Gray, S. rigidus, S. pumilus Vahl, S. Clementis, S. cespitosus L., S. cespitosus var. callosus and S. atacamensis. Three members of this group have a circumboreal distribution, and the fact that this is an old group is attested by the obvious relationship of two Andean endemics to these northern types. Both Scirpus cespitosus var. callosus and S. hudsonianus are found in North America, Europe and Asia. Scirpus pumilus occurs in a few isolated stations in North America, in Europe and has been reported from Tibet The end points of migration down the Rocky Mountains, (5).through the montane regions of Central America and into the Andes, are represented apparently by S. rigidus of Peru and Bolivia and S. atacamensis of Chile and Argentina.

That Scirpus planifolius and S. Clintonii are most closely related, within the section Baeothryon, to S. hudsonianus is shown by their mutual possession of cauline leaves and scabrous triangular culms, and is also strongly indicated by the roughly equiformal areas of their North American distribution. On the same morphological grounds the South American S. rigidus is more closely related to these three and less closely allied to its geographical partner S. atacamensis. The last species has smooth, terete culms and cauline leaves reduced to mucronate sheaths, conditions which demonstrate its affinity with S. Clementis and S. pumilus. Acceptance of the latter assumption makes it necessary to postulate one of two possibilities as to their geographic origin: (a) a double migration down the Andes from North America; (b) a continuous range from North to South America for some prototype which has diverged along parallel lines of evolution subsequent to the geographic isolation of some of its parts. In either case the history of the plants undoubtedly dates back to the Pliocene when, coincident with the earliest invasion of South America by holarctic fauna (6, 9), one or more of the species may be assumed to have had its widest distribution. Fernald (4) has pointed out that the present fragmentary distribution of *Scirpus pumilus* is probably a direct result of Pleistocene glaciation.

Various species in other sections of the genus show an interruption of their ranges in the tropics. *Scirpus nevadensis* is found to be an uncommon plant in the western United States and Canada occupying strongly saline soils over a wide area. It is rare in

hemispheres.

Argentina where it also appears in strongly saline habitats over a wide area. The species is, however, unreported between northern Argentina and Mono County, California. It may have been a coastal, salt marsh type or perhaps was formerly tolerant of fresh or only slightly saline water. Analogies exist today in S. palu-dosus, S. americanus, and S. acutus which grow on the sea margins, on the borders of inland fresh-running streams and lakes and in the saline soils of the Great Basin. The uplift of the Rocky Mountains and the Sierra Nevada initiated the changes which resulted in the disappearance of some of the inland lakes and increased the salinity of others. Gradually, in accompaniment with this change, S. nevadensis may have developed an adaptive tolerance toward aridity. The southern members of the species may have passed through a similar history but the members between were faced with a different problem; either they disappeared or gave rise to such closely related species as S. Olneyi and S. americanus.

Scirpus paludosus, S. validus and S. Olneyi are similar to S. nevadensis in the interruption of their ranges by a broad belt of the tropics including at least Central America and South America north of the Amazon but they differ in being much more abun-dant in North America than in South America. There are several possible explanations to account for the existence of this broad hiatus in distribution which is certainly not a reflection of incomplete collections: (a) the species may be spreading from the northern to the southern hemisphere and have not yet had time to occupy all of their potential area; (b) these species may, perhaps, have been more abundant in the past but are becoming depleted in the southern hemisphere due to the impact of changing conditions; (c) greater competition in the southern hemisphere flora may possibly have hindered the spread of these species since they first appeared there; (d) since they are not especially tolerant of tropical conditions a migration through that area may have been accomplished by a few of the more tolerant biotypes. Scirpus paludosus and S. validus are evidently plastic species to which the first alternative may be applicable but S. Olneyi appears to be a more rigid type and the other alternatives may have to be called into account.

Scirpus cubensis which is common in Chile is reported also from Panama by Standley (10). Scirpus inundatus, known from as far south in Chile as the Valdivian Lakes region is also reported from Costa Rica by Clarke (3, p. 460). Scirpus cernuus, a ubiquitous species with a world wide distribution in temperate regions avoids the tropics.

Scirpus californicus and S. americanus also have a disrupted range but differ from the preceding species in being widespread and fairly common in both hemispheres. They come nearest to bridging the tropical barrier. Scirpus californicus is known from the San Francisco Bay region south to Guatemala, and from Colombia, Ecuador and Brazil to middle latitudes in South America. To this is added S. californicus var. tereticulmis (Steud.) comb. nov. (S. tereticulmis Steud. Syn. Pl. Cyp. 85. 1855) extending the total range from central South America to the Straits of Magellan. A more uniform climate would undoubtedly amplify this broad latitudinal range. There is geological evidence (2) that uniform, moist climates existed at several different periods of Tertiary time.

Scirpus americanus, finally, is known from Nova Scotia and Alberta south to Mexico and from Peru and Brazil to Patagonia. Morphologically similar plants grow indiscriminately in fresh and strongly saline waters. The extreme variability in this species is suggested by the number of taxonomic variations which have been recognized in it. Such a high degree of polymorphy would seem to mark it as a comparatively young species which is reaching the peak of its distribution at the present time.

There has now been presented a graded series of geographical distributions from the endemics of section Baeothryon on the one extreme to the ubiquitous Scirpus americanus on the other. The most widely ranging species in the series are those with the greatest variation. This fact suggests that at the time when its number of biotypes and range of tolerance is greatest it is possible for a species to cross well-marked climatic barriers. Probably S. Clementis and S. atacamensis together represent an old species which, with advancing age, depauperization of biotypes and wide separation, became modified in descent to slightly different end points. Since they occupy areas isolated from other members of their section this assumption seems more reasonable than to suppose that they never had a sufficient wealth of biotypes to create an overlapping of their now discrete ranges; that is, chance dispersal or fortuitous origin depend on close relatives living in nearly adjacent territories. The species whose distributional pattern is intermediate in character between those of S. Clementis and S. americanus may be classed logically as intermediate in age if they no longer occupy their maximum range, or as young species if they have yet to reach a maximum range.

The methods of dispersal of *Scirpus* are not yet completely Most species are stoloniferous perennials which mianalyzed. grate easily either up or down stream along muddy river banks. Birds eat the fruits and may carry them for short distances, that is, from one drainage area to another, in their digestive tracts, or in mud adhering to their feet. Undoubtedly important also is the buoyant nature of the fruits, although this is an extremely variable factor. Achenes of S. americanus are considered to be non-buoyant but are abundant in lake drift (7) while those of S. maritimus L. may float for a month (8, p. 239), not sinking until the pericarp Finally the element of chance dispersal undoubtedly decays. plays a considerable role over a long period of time. The prevalent uniformity of the aquatic habitat must be largely responsible for the high degree of relationship over wide areas.

A conclusion similar to that reached by Matthew (6) in connection with a study of the evolution of land vertebrates may be It would seem to be unnecessary to postulate any prodrawn. found change in the existing distribution of land masses to account for the present distribution of Scirpus between the two hemi-To assume change in climate is probably unnecessary spheres. since species are apparently being interchanged between North and South America at the present time, but a more uniform climate would facilitate this process. Such changes as did occur in the past certainly have had their effect on the history of the species concerned, but, apparently, any theory involving cataclysmic phenomena is not essential to account for the migrations of North and South American species of this genus.

> Department of Botany, University of California, Berkeley, March, 1940.

LITERATURE CITED

- 1. BARROS, M. Ciperaceas Argentineas. Anales Museo Arg. Ciencias Nat. 38: 133-172. 1935. CHAMBERLIN, T. C. A group of hypotheses bearing on climatic changes.
- $\mathbf{2}$. Journ. Geol. 5: 653–683. 1897.
- 3. CLARKE, C. B. The Cyperaceae of Costa Rica. Contrib. U. S. Nat. Herb. 10: 443-471. 1908.
- 4. FERNALD, M. L. Persistence of plants in unglaciated areas of boreal America. Mem. Acad. Arts & Sci. 15: 266–268. 1925.
- 5. HOOKER, J. D. The Flora of British India. 6: 654. 1894. 6. MATTHEW, W. D. Climate and evolution. Annals N. Y. Annals N. Y. Acad. Sci. 24: 171-318. 1915.
- 7. MCATEE, W. L. Notes on drift, vegetable balls, and aquatic insects as a food product of inland waters. Ecology 6: 288-302. 1925.
- 8. RIDLEY, H. N. The dispersal of plants throughout the world.
- 9. Scott, W. B. A history of land mammals in the western hemisphere. Rev. ed. 1937.
- 10. STANDLEY, P. C. Flora of the Panama Canal Zone. Contrib. U. S. Nat. Herb. 27: 90. 1928.

THE PROBLEM OF LIFE ZONES ON MOUNT SHASTA, CALIFORNIA

WILLIAM BRIDGE COOKE

In 1898 a party led by Dr. C. Hart Merriam made a biological survey of Mount Shasta. In the report (6) published in 1899 Dr. Merriam defined the several life zones he found on the mountain on the basis of his earlier discussion of North American life and crop zones (5). The writer, after four years of study, has come to the conclusion that two of the three zones must be revised or clarified (or, as to one of them, completely eliminated) in order that the casual visitor and future worker may be less confused as to the boundaries of the upper zones. The present paper is an